

PRIMITIVE NERVOUS SYSTEMS. CONTROL AND RECOVERY OF
FEEDING BEHAVIOR IN THE POLYCLAD FLATWORM,
NOTOPLANA ACTICOLA

HAROLD KOPOWITZ, DAVE SILVER AND GREGORY ROSE

Developmental and Cell Biology, University of California, Irvine, California 92717

Turbellaria are usually considered to be the most primitive animals which possess a brain. But, despite its strategic phylogenetic position, very little is known about flatworm brain function. Available evidence suggests that flatworm brains have mainly a coordinatory function and that the basic motor neurones underlying specific patterns of muscular activity occur in the peripheral nervous system (Loeb, 1894; Gruber and Ewer, 1962; Koopowitz, 1970, 1975a). The African polyclad *Planocera gilchristi* is able to recognize and ingest prey in the absence of the brain, as can the Californian polyclad *Notoplana acticola*. Not all polyclads, however, possess this ability, and worms such as *Enchiridium punctatum* which have a tubular rather than plicate pharynx cannot feed unless the brain is present. One generally suspects that behavior in primitive organisms should consist of simple reflexes without much plasticity, but our analysis of feeding behavior suggests that this is, in fact, not the case. What may appear to be smooth simple behavior can be made up of a series of peripheral events with variable central control superimposed on separate systems.

This paper reports on the components of feeding behavior in *Notoplana acticola* and presents a behavioral study which precedes work on the neuronal basis of feeding in this species. As an outgrowth of this study it was found that repair to lesions in the nervous system was very rapid, and certain aspects of recovery of function have therefore also been investigated. A surprising finding is the amount of plasticity in the system. Alternative pathways can be used to convey information to the brain in the event that the normally used pathways are disrupted. A preliminary report on part of this data has already been published (Koopowitz, Silver and Rose, 1975).

MATERIALS AND METHODS

Specimens of *Notoplana acticola*, approximately 1-2 cm long, were collected from tide pools at San Onofre, California. Animals were kept in 11 cm diameter finger bowls which contained 2.5 cm of sea water. Water was changed after a daily feeding of brine shrimp, *Artemia salina*. Ambient laboratory temperature was between 18° and 20° C. No aeration was required. Individuals have been kept in good condition for over six months.

All lesions were made while animals were anesthetized with a 50% solution of .36 M MgCl₂ in sea water. Animals recovered and would eat within one-half hour of surgery. Decerebration was performed by punching the brain out with a capillary tube (internal diameter 1 mm). It could be determined that the brain

was in fact removed by inspection. In all experiments, animals were tested by holding a brine shrimp next to the part of the margin under investigation. The worms were not allowed to swallow the shrimp during testing.

Removal of part or all of the margin was used to determine the location of the chemoreceptors. Animals were then tested on the cut and noncut portions of their periphery. Observations on responsiveness were made daily until the margin had regrown.

Recovery of function experiments used a cut made through the entire body, from the midline of the animal to the margin. After lesioning, observations were made while holding a shrimp behind the cut on the lesioned side or at the same level on the control side. The response to food is a localized extension of the margin next to the shrimp and the food is gripped firmly by the margin. In an intact animal or on the control side, the animal makes an ipsilateral turn and food is transferred to the anterior margin from where it is passed back towards the mouth. An ipsilateral turn towards the food was scored as a turn (T) if the anterior margin came in contact with the food. In decerebrate animals or where food was offered behind an unhealed cut there was still localized extension and gripping of the food. No ipsilateral turn occurred and food was passed directly forward towards the mouth. Localized extension and gripping of the food was scored as a local feeding response (LFR), when it was not followed by an ipsilateral turn. In a scored LFR the worm attempted to move the food directly to the mouth, but it should be pointed out that recognition and gripping of food by the margin is essentially the same whether or not there was a turn. Results were expressed as the percentage of turns for an individual side. Usually ten readings were obtained from each side. As one side of the animal acted as control for the other side, food was offered to each side alternately. In the above experiments the food was always removed before it could be swallowed.

Sections were examined with a microscope and stained with Samuel's silver stain (1953). Samuel's stain is excellent for portraying neuronal tissue in polyclads, but unfortunately the harsh treatment administered during staining tends to affect other tissues adversely. Methods used for ultrastructural preparation and examination have been reported previously (Chien and Koopowitz, 1972).

Electrophysiological techniques involved the use of polyethylene suction electrodes. Recordings were made directly with a 3A9 verticle amplifier and a 565 Tektronix CRO. A Grass S44 electronic stimulator and Grass photoisolation unit were used to provide constant current square wave stimuli.

RESULTS

Feeding behavior in normal animals

When *Notoplana* is offered a brine shrimp at its anterior margin, that portion of the body closest to the shrimp is extended toward it. The edge of the margin grips onto the prey which is then conveyed to the midventral mouth where it is ingested. A flatworm which has been starved for one or two days will make a rapid lunge at the food and grip onto it. Animals which have been fed daily and

routinely do not strike at their food. The margin closest to the food is raised above the substrate and extended towards the food. During feeding the tail end of the animal grips the substrate.

If a shrimp is offered to the posterior lateral margin of the worm, it will lift that sector of the edge and grip onto the food. This is followed by an ipsilateral turn which brings the anterior margin of the flatworm into contact with the food (Fig. 1a). The posterior lateral grip is relaxed and the food transferred to the anterior margin which grips it and then passes the food posteriorly toward the mouth. A hungry *Notoplana* will accept and eat three to five adult brine shrimp in less than five min but will not feed again for at least three-fourths to one hour. Any food offered during this satiated period will be ignored and even the initial margin extension will not occur. Toward the end of the satiated period the margin may extend and investigate the food but usually will not grip it. If it does hold

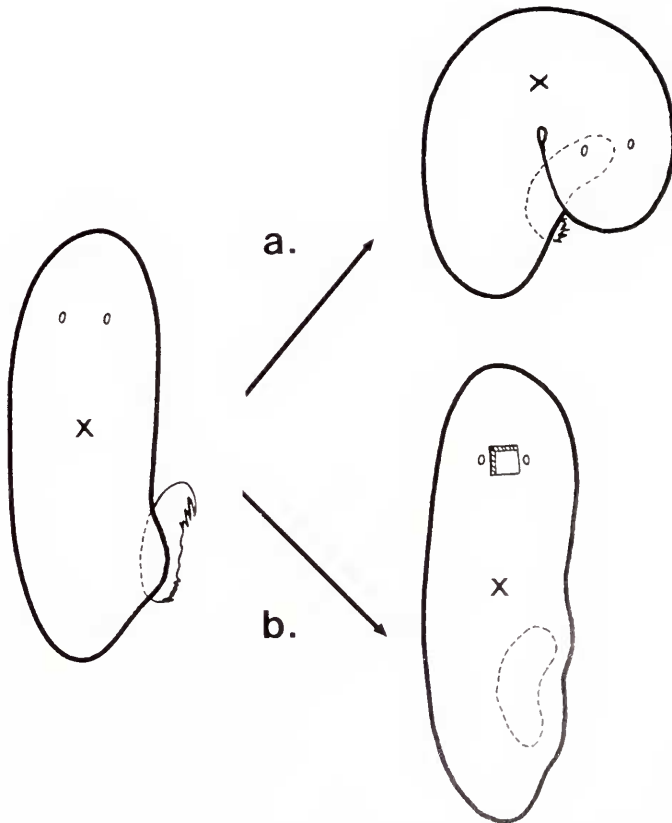


FIGURE 1. (a) Normal feeding patterns in *Notoplana acticola*. Following local extension there is an ipsilateral turn and food is transferred to the anterior part of the worm and then conveyed to the mouth. (b) Feeding in a decerebrate worm involves prolonged extension and food is conveyed directly to the mouth. Position of the ventral mouth is marked with an X.

onto the food it will not swallow it, even after the satiated period is over and after it accepts and ingests food offered to other parts of the margin.

Decerebrate feeding

There were a number of differences between normal and decerebrate animals in their feeding behavior. When shrimp was offered to the posteriolateral margin of an animal without its brain, the margin was extended and the prey held. There was no gripping of the substrate by the tail. The food held by the edge was then conveyed directly to the mouth where it was swallowed (Fig. 1b). No turning occurred. Shrimp offered to the anterior portion of the animal was accepted and passed posteriorly to the mouth. These local feeding responses (LFR) continue as long as food is offered. A decerebrate flatworm will accept so many shrimp that it cannot swallow all of them and its body will be lifted off the substrate until it is lying on top of a pile of food. Clearly, the usual satiation reflexes are not brought into play in a decerebrate animal.

A cut directly through the animal's body from the midline to the margin leaves that ipsilateral portion posterior to the cut without central control. Food offered here evokes an LFR without turning, whereas food offered to the contralateral side evokes ipsilateral turning. The portion behind the cut will continue to pass food directly to the mouth for ingestion, long after the contralateral side has become satiated. The fact that the mouth continues to swallow food provided to the cut side, after the intact portions act satiated, suggests that satiation works peripherally and blocks the LFR.

Sensory aspects of feeding

The receptors responsible for feeding behavior seem to be scattered all along the margin of the worm, as a shrimp placed in contact anywhere along the worm's margin will elicit feeding. If the entire margin is removed the animal will not feed. As a partial control to the considerable injury forced on the animal in these experiments the entire posterior third of each of a group of worms was cut off. These flatworms would feed within five minutes of being injured, whereas worms with entire margins removed did not start feeding until about five days after the surgery. Animals with only twenty per cent of the margin intact would feed if food was presented to the intact portion. Experiments with less than twenty per cent intact were not performed. It seems reasonable to assume that the receptors which initiate feeding are confined to the margin of the worm. Worms without a margin do not respond to shrimp even if the food is placed in contact with the cut edge or dorsal surface. Animals will ignore food offered to areas where only a very small portion of the margin has been cut away, as long as it does not come in contact with an intact edge. The lateral portion of the animal at the level of the eyes appears to be the most sensitive area. Feeding behavior is much more vigorous and rapid when food is presented at this region. Hungry animals will respond to vibrations in the water near them. A starved animal will attack an inert object such as a glass rod if it is moved near the animal. The worms, however, are able to differentiate between vibrations and chemical stimuli. If two

glass capillary tubes, one filled with sea water and the other with shrimp homogenate, are presented to a worm together they will always choose and hold onto the tube filled with shrimp homogenate.

Normal feeding behavior requires stimulation of two sets of marginal receptors. When food is presented along the side, the lateral receptors are necessary to initiate turning. Anterior receptors are necessary for the pattern needed to convey the food to the mouth. In the following experiment a group of worms had the anterior portion of the margin excised. The next day these flatworms were presented with food to a posterior lateral margin. All the worms gripped onto the food with the posterior lateral edge and an ipsilateral turn was initiated which brought the emarginated anterior edge into contact with the food. In all cases the worms released the shrimp with the posterior margin but did not grip onto it with the anterior edge. The food was not conveyed to the mouth and these animals would not feed. They consistently moved away leaving the shrimp behind. Animals which have the nerve trunks leading to the brain cut pass food directly from the lateral margin to the mouth whereas animals which have the anterior margin removed will not feed with an LFR. This apparent inconsistency makes sense if one assumes that the central nervous system usually inhibits motor pathways involved with conveying food directly from the side to the mouth.

Previous study on the tactile system in *Notoplana* (Koopowitz (1975b) indicated that sensory information reached the brain through a diffusely conducting nerve net. The chemosensory system involved in feeding, however, appears to utilize specific routes. Cuts parallel to the margin, between 4 to 5 mm long and 1 mm from the edge of the margin, were made. The cuts were positioned in the middle of one side and were deep enough to cut right through the animal. When shrimp were offered to the margin flanked by the cut the strip of margin responded by gripping onto the food. However, no turning occurred, and the food was not conveyed to the mouth. Food offered on the uncut side evoked the turning response as would food offered on the cut side where the receptor area was not flanked by the cut.

Recovery of feeding behavior

In experiments where cuts had been made through one side of the body it was noticed that animals started to turn after a period of recovery. This was examined in more detail in the following experiment (Fig. 2a).

A series of ten worms were tested for turning towards a shrimp offered to the posterior lateral margin. All animals initially turned to both sides. In these experiments each animal was tested ten times and the form of the response was noted. The animals were then cut on one side of the body. Each lesion extended from the midline to the margin and cut right through the body. The cut was positioned halfway along the animal's length. When animals were tested for turning before the cut had healed, it was found that the control side turned most of the time and the response to food offered posterior to the cut evoked an LFR. After the cuts had healed both sides responded to food with ipsilateral turns. In order to test whether or not the nerves which were originally cut had reconnected

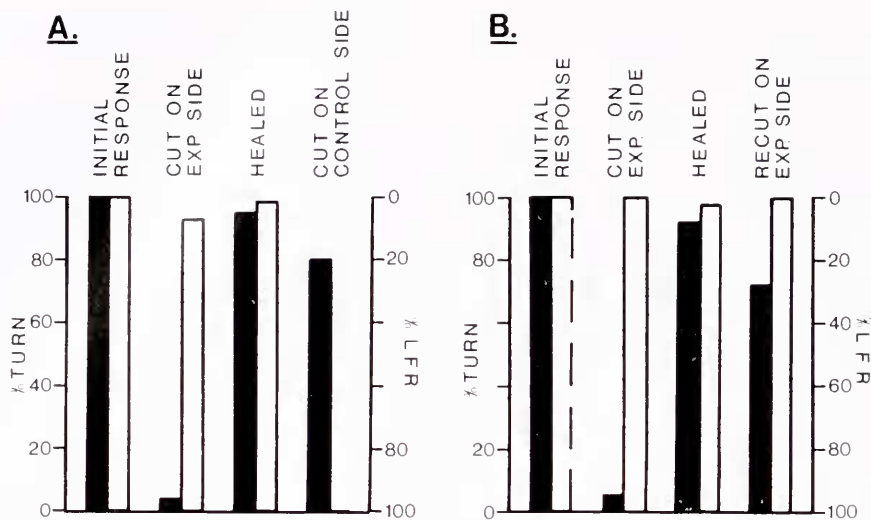


FIGURE 2. (a) Recovery of feeding behavior following lesions through one side of the animal. The black bar of the histogram is the cut side and the white bar is the control side. Treatment is written above each set of bars. Readings on healed animals were made 49 hr after the initial cut. (b) Recruitment of contralateral pathways. Experiment was the same as in (a) except that the animals were then recut on the experimental side. Healed readings were made 46 hr after the initial cut. The initial response readings were not taken on the control sides and here it is assumed that a response of approximately 100% turn would have been recorded.

in a physiologically meaningful way, another cut was then made across the control side and the animals then were retested. Now, the cut control side only responded with LFRs, but, rather surprisingly, the number of turns on the healed experimental side dropped from 94.9% to 79.8%. Close examination of the above data revealed that the drop in turning frequency was due to consistent use of LFRs by two of the worms. There appears to be three possible explanations for the re-appearance of turning behavior. The nerves could have become reconnected; new or little-used tracts across the other side of the body could have been recruited; or thirdly, mechanical coupling across the cut could have stimulated some type of stretch receptor which would then have initiated turning.

Although the data in the above experiment suggested that pathways could be reestablished across a lesion, the other two possibilities were not ruled out. A further experiment was performed (Fig. 2b), similar to the first. Ten animals were tested and then cut on one side. After the cuts had healed and turning had been reestablished, the original cut was then reopened. Turning on the healed side dropped from 92.1% down to 72.1% when the cut was reopened. All the animals turned but seven worms also responded with LFRs. Whereas turning only took 1-5 sec in healed animals, it now took at least 20 sec to become initiated in reopened flatworms. Subsequent serial sectioning revealed that in all but one animal all the nerves on the healed side of the body had been resealed. The results of

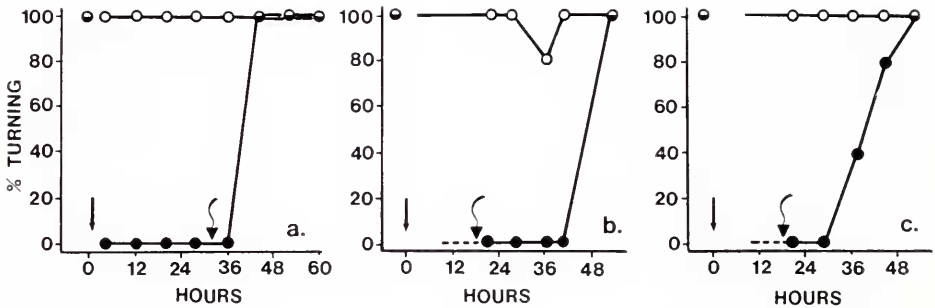


FIGURE 3. Patterns of recovery following lesions on one side. Each graph represents the performance of an individual animal. The straight arrow is the point in time when the side was cut and the curved arrow the point in time where the edges of the cut appeared to have healed. Open circles are the response of the control side and closed circles are the response from the experimental side. All axes are the percentage of turns recorded. (a) The most common pattern of healing; (b) and (c), unusual patterns seen in two individuals.

both experiments clearly show that not only can nerves rejoin to produce functional behavior but that pathways can be recruited to take over the functions of those which have been damaged. The fact that turning occurs following reopening of the cut also indicates that mechanical coupling across the cut is not a prerequisite for turning.

Time course of recovery

Recovery of ipsilateral turning behavior was followed by offering food at approximately 8 hr intervals to animals which had been cut through on one side. The most common pattern of recovery, found in six out of nine cases, is displayed in Figure 3a. Following surgery the experimental side responded with LFRs. The cut edges of the body rejoined in approximately 32 hr and the animal started to turn 100% of the time some 8 to 12 hr later. Two other patterns also occurred. In small animals the cut edges often rejoin shortly after cutting; but in one case followed, turning did not commence until 32 hr later (Fig. 3b). Usually, once turning occurs it does so nearly 100% of the time. One preparation, however, showed a gradual acquisition of turning (Fig. 3c). An important point brought out by these experiments was the fact that mechanical coupling across the cut edges seemed unimportant. There was always a delay between healing and the resumption of turning behavior.

The time course for recovery of function across the other side of the body was also followed. In this series of experiments the cut was not allowed to heal and the reappearance of turning behavior was monitored. If the edges of the cut rejoined then it was reopened as soon as noticed. These experiments turned out to be difficult to perform as worms seemed unable to tolerate all of the handling and cutting required. Of some 20 animals, 9 became completely unresponsive and could not be used. The other eleven all turned in response to food. Figure 4a is representative of the pattern of recovery seen most frequently. Animals started

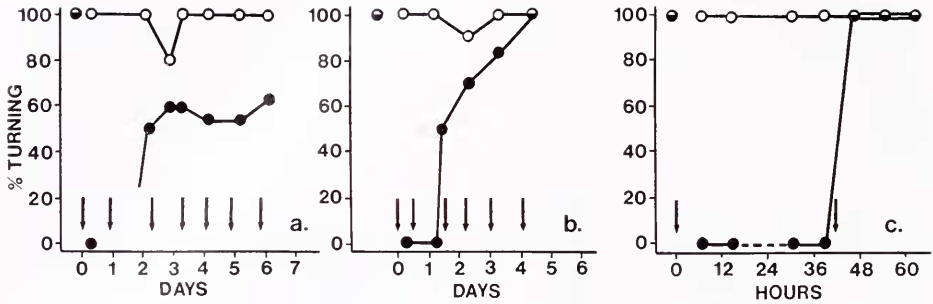


FIGURE 4. Recruitment of contralateral pathways. Each graph represents the performance of a single individual animal. In these experiments the cut was not allowed to heal. Each straight arrow represents the time when the cut was reopened. Closed circles are from the experimental side of the worm and the open circles are from the control side. (a) The most common pattern obtained. Here the animal does not achieve 100% turning during the length of the experiment. (b) A gradual improvement of performance was seen in a number of worms. (c) Abrupt acquisition of normal behavior was only seen in one preparation. The dashed portion of the line represents time during which the animal was not responsive.

turning approximately 48 hr after the original cut had been made. Characteristically these flatworms only respond with ipsilateral turns part of the time. Where acquisition of 100% turning occurs there is a gradual buildup of the effect so that it may take four or five days before this percentage is reached (Fig. 4b). In one unusual case (Fig. 4c), the animal turned 100% of the time as soon as it had recovered the behavior.

Anatomical considerations

A series of worms were examined, histologically, to see if severed nerves had rejoined. Animals were cut on one side and as soon as ipsilateral turning in response to food was reestablished the animals were fixed and sectioned. Examination of healed cuts at the light-microscope level clearly reveal nerve trunks which course across the scarred zone (Fig. 5a). Although the severed nerves realign themselves, the contents, especially of the larger trunks, tend to take on a 'bubbly' appearance (Fig. 5b). Samuel's silver stain (1953) tends to stain the outer edge of nerve axons in flatworms, and the vacuolated appearance of the trunks in the region of the scar may represent swollen tips of cut axons. Attempts to verify this or locate severed stumps at the electron-microscopy level have been unsuccessful as the scars themselves tend to be wider than the section diameters and we cannot distinguish between neurites anterior or posterior to the cut. The neuroglia in these sections are enlarged and contain much in the way of myelin bodies. Obvious degenerating axons also occur. At present one cannot recognize if two severed axons fuse together or if new processes grow out.

Conduction across healed nerves

It has been demonstrated that recovery of behavior occurs and that this is accompanied by morphological repair of the nerves. It also remains to be shown that

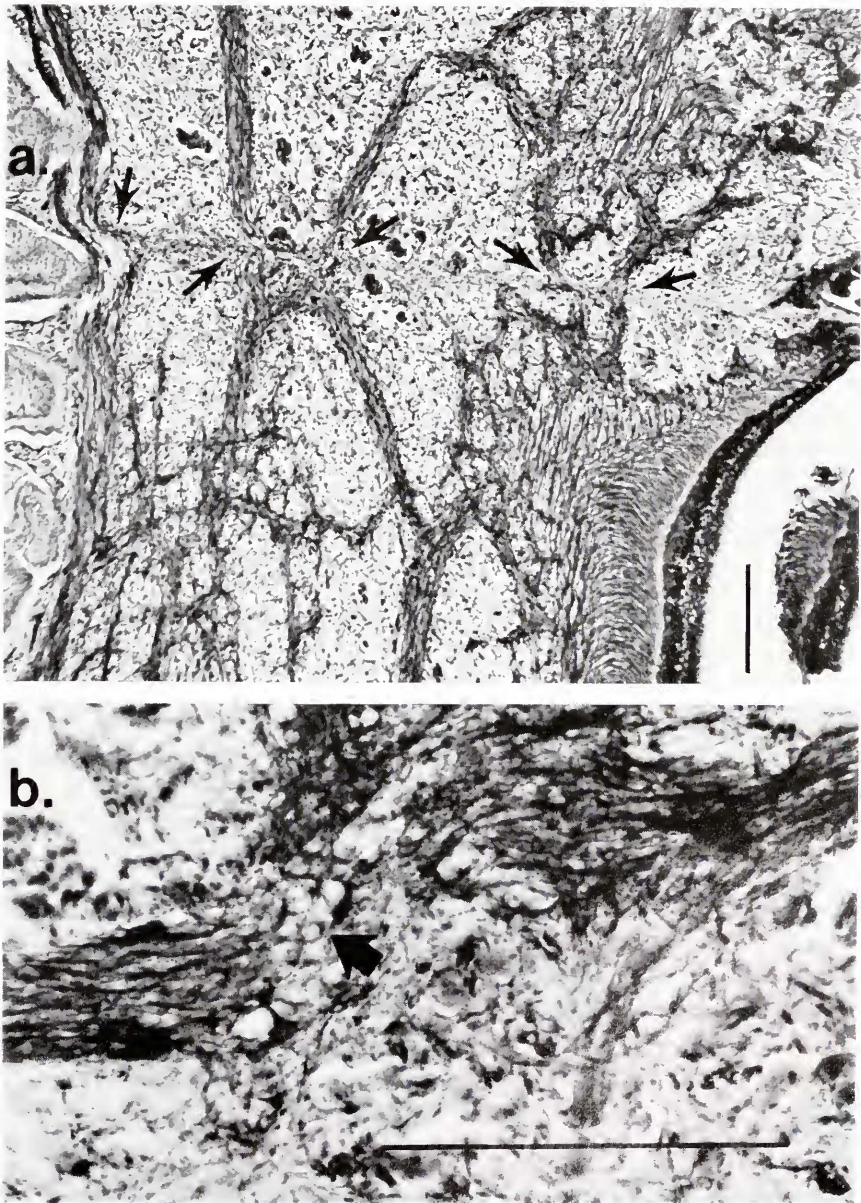


FIGURE 5. Section through a healed cut after turning had been reestablished. (a) Portion of the ventral submuscular plexus. Nerves in the region of the scar are indicated by arrows. (b) A single nerve trunk from another preparation to show the 'vacuolated' region of the nerve at the level of the scar, indicated by an arrow. Nerves silver-stained by Samuel's method (1953). The bar equals 200 μ .

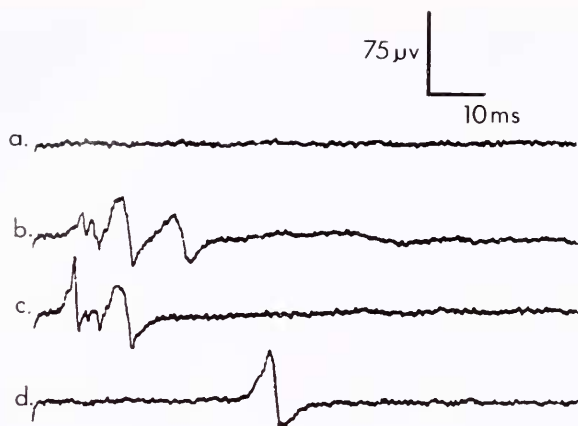


FIGURE 6. Recordings from rejoined nerve trunk. The stimulating electrode was distal to the healed part and the recording electrode proximal. (a) Single below-threshold shock of 6 volts. (b) Response to an 8-volt stimulus. (c) Response to a 10-volt shock. (d) Recording to a 10-volt stimulus after the cord had been severed between the electrodes. The potential recorded here is probably from the Mg^{++} insensitive net.

repaired nerves are able to conduct potentials across the scar. Animals which had been cut and then demonstrated recovery of behavior were selected, and the following experiment was conducted.

The flatworm was anesthetized in 50% $MgCl_2$ isotonic with sea water. Two positions on the major longitudinal nerve were exposed and cleaned so that suction electrodes could be applied to the nerve. One position for recording was close to the brain and the other for stimulating was a considerable distance behind the healed cut on a level with the genitalia. The nerve was then severed between the electrode and the brain to eliminate possible feedback from the brain. In two of three preparations, a short latency compound action potential was recorded which had a definite threshold. This potential was conducted across the healed cut (Fig. 6b and c). In all three preparations slow single unit spikes could also be elicited, but these appeared to be conducted more slowly (Fig. 6b). In the two preparations which showed compound potentials, the nerve trunk was cut between the two electrodes. Following this the compound potential disappeared but the single unit activity remained (Fig. 6d). The unit activity remained even after the cut had been continued through the contralateral cord and into the other side until a strip of margin only 1.0 mm wide remained. The activity was lost when this strip was cut too. There is no assurance or evidence that the major longitudinal trunk is used during the initiation of turning during feeding, but the experiment clearly shows that functional physiological repair of nerves can occur.

DISCUSSION

Although the neuronal pathways concerned with control of feeding behavior are not yet known, it is possible to construct a model of the kinds of systems which

one might expect to find (Fig. 7). Stimulation of the receptors leads to an LFR which in a normal animal gives way to an ipsilateral turn and tail grip on the substrate. These events appear to require the brain or pathways which lead to the brain. The LFR can be inhibited or depressed in either of three ways: when the animal turns; during rapid forward locomotion; and when the animal is satiated. We have not been able to determine if these use a common pathway from the brain or if there might be separate nerve tracts involved. In a brainless animal, an LFR can be evoked at any position around the margin which suggests that numerous reflexes must be built into the peripheral plexus. Sensory pathways from the receptors appear to utilize direct pathways to the brain rather than a nerve-net such as used in conduction of tactile information to the brain (Koopowitz, 1973, 1975b). This makes physiological sense as positional information is needed to direct the anterior portion of the animal during the ipsilateral turn. Tactile information, on the other hand, appears to be a general alerting sensation, and direct positional information is in that case relatively unimportant.

The hierarchical arrangement between feeding and locomotion in *Notoplana* is of some interest. Behavioral hierarchies involved with feeding have been clearly demonstrated in the mollusk, *Pleurobranchaca* (Davis, Mpitsos and Pinneo, 1974a and b), but similar hierarchies have received little attention in the lower metazoa. What is of considerable interest here is that differential inhibition of parts of the feeding response occurs. Ditaxic locomotion, in *Notoplana*, depresses different

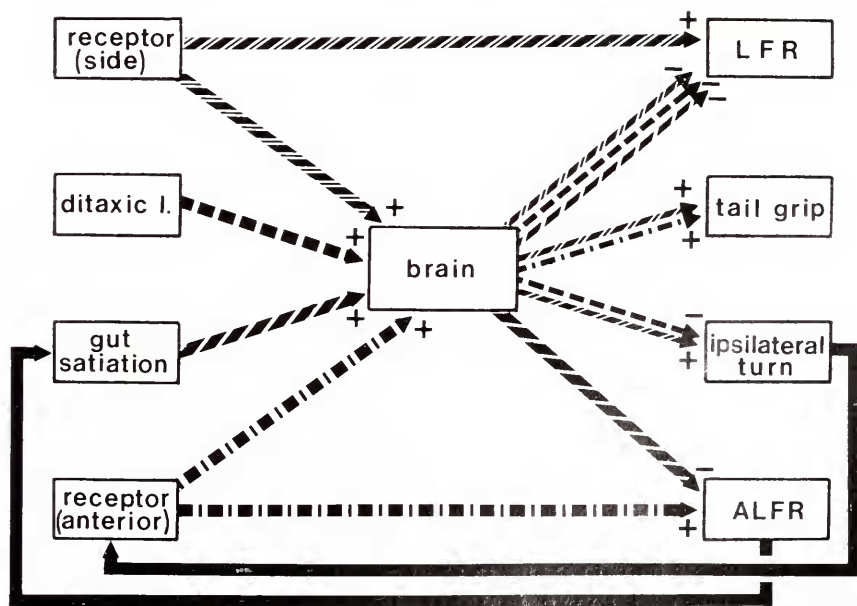


FIGURE 7. Pathways involved with feeding in *Notoplana acticola*. Pattern on the line indicates source of the pathway. Solid pathways are not neuronal but behavioral. Multiple pathways are shown rather than common pathways, as this allows one to identify the origins of the component; but there is no information on the actual anatomical pathways.

patterns of the total feeding behavior, depending on how vigorously the flatworm is moving. It is difficult to obtain quantitative data which clearly illustrate the hierarchical nature of inhibition but the following series can be observed. An animal indulging in escape locomotion to a noxious stimulus ignores all food stimuli as will other animals which merely appear to be moving rapidly for no apparent reason. On the other hand, an animal moving moderately fast will usually respond to food offered anteriorly and feed, but if food is offered posteriolaterally there is no response. A worm moving slowly will also accept food offered to the posteriolateral margin but feeds with an LFR; there is no ipsilateral turn. Non-locomoting worms nearly always turn.

Feeding behavior involves a chain of reflexes which are not necessarily neuronally connected. Quite clearly the transfer of food to the anterior part of the animal following an ipsilateral turn requires not only inhibition of the LFR but also stimulation of the anterior receptors. Similarly the initiation of inhibition of feeding with satiation is also dependent on a behavioral link in the chain rather than a neuronal connection. Animals will feed many times on small pieces of shrimp but only respond a few times when given large pieces. Little difference is seen between normal and decerebrate animal feeding when food is offered anteriorly. Consequently it is not possible to determine if the behavior following an ipsilateral turn is determined by central rather than peripheral neurones. Certainly the presence of a peripherally-based network underlying the anterior LFR does not preclude central neurones also.

Not reported in the results section are several attempts to isolate a molecule or molecules which might initiate feeding behavior, but certain comments might be useful at this point. Similar attempts to isolate a molecule that caused pharynx eversion in freshwater planarians (Ash, McClure and Hirsch, 1973) suggested that it might have a molecular weight of between 700–2000. They found that the molecule was not denatured following one min of boiling, and that it resisted both α -chymotrypsin and protease digestion. It is possible to separate out the vibration receptor response from that of the chemoreceptors by offering the animals pairs of capillary tubes, one filled with sea water and the other filled with the test chemical. The flatworms will accept seawater-filled tubes if offered alone; but if one tube is filled with brine shrimp homogenized filtrate, that will be chosen in preference to sea water. In fact, the tube with sea water will be ignored. Using ultra-filtration (Amicon UM-2 and UM-10 filters) it was determined that the molecule was larger than 1000 mol wt. We also found that boiling for 30 min had no effect. On one occasion protease digestion at 29° C destroyed most activity. Unfortunately, these results could not be repeated. The specific molecule or molecules could be further separated on a Sephadex column (G-25) and when the effluent was tested using paired capillary tubes, animals responded positively to samples in the 2000–5000 mol. wt. range. There is, of course, no assurance that the planarians and *Notoplana* might be responding to the same molecule.

Regeneration is well known in the turbellarians but many polyclads have limited powers of repair, and the brain seems to be necessary for this to take place (Olmstead, 1922). *Notoplana* will only survive for a few days if the brain is removed. Not all recovery is as rapid as turning behavior. Ditaxic locomotion

in *Notoplana* appears to require the two sides of the brain intact. If the brain is bisected, animals are unable to locomote properly and recovery of locomotory behavior takes about five days to occur (J. Faisst, University of California, Irvine, personal communication). One of the major questions to be answered is whether or not the repair is due to regeneration of the axons or axonal fusion between the severed stumps.

Work on leech ganglion and cord suggest that anatomical connections formed during repair are specific between certain cells but the physiological junctions may have altered properties (Baylor and Nicholls, 1971; Jansen and Nicholls, 1972; Jansen, Muller and Nicholls, 1974). Functional repairs take considerably longer in leeches than in polyclads but axo-axonal chemical synapses appear within four days between the severed ends of axons (Fernandez and Fernandez, 1974). In crayfish Hoy (1973) has presented considerable evidence that fusion between the cut ends of axons probably occurs. Evidence for this is the rapid reappearance of behavior, within two weeks, although degeneration times are much slower. In fact severed axons in Crustacea appear to remain functional for considerable periods of time and signs of degeneration are only found in about 1% of crayfish claw nerves during the first four weeks, although the glial cell morphology associated with the severed axons had changed (Nordlander and Singer, 1972). Initial ultrastructural investigations revealed a large number of myelin bodies in the glia; this is often associated with degeneration, but without further investigations the kind of repair which occurs in *Notoplana* can not be determined.

Initially, the rapidity of recovery would seem to preclude regeneration and growth of new terminals in favor of axon fusion. If regeneration occurs at a rate of 170 μ /hr [which appears to be a maximum growth rate of axonal growth in vertebrates (Jacobsen, 1970)], then within 8 hr of the cut healing, the regenerating neurites would only have traversed 1.36 mm. As the brain usually lies about 1.5 cm anterior to the position of the cut, it would seem that growth of sensory axons to the brain could not account for repair unless growth rates were considerably faster or if synaptic connections were made close to the site of the cut. It should be pointed out that these experiments were recorded in Mg^{++} enriched saline and were close to the brain; nevertheless, potentials were transmitted to the electrode. In other neurophysiological preparations, it might be assumed that one was recording from continuous axons because synapses should be blocked by the Mg^{++} ions. The nerve net in some polyclads, such as *Frcmania* and *Notoplana* (Koopowitz, 1975b), is insensitive to magnesium ions although certain central and neuromuscular junctions are blocked. It is possible, therefore, that Mg^{++} insensitive connections were formed. An interesting observation obtained while recording from the ventral longitudinal nerve trunk was the presence of the diffusely conducted spike. Although this potential cannot be tied to a particular behavior it shows that potentials can be fed into the longitudinal tract through the diffusely conducting system, and that these function in high Mg^{++} concentrations. Whether this type of system is involved with rerouting of sensory information across to the other side of the body is unknown. The possible presence of Mg^{++} insensitive synapses precludes simple interpretation of the data, and deciding if recovery involves axon fusion or regeneration or both must await further work.

SUMMARY

1. Feeding behavior in *Notoplana acticola* involves a series of local responses which are under central control. Behavior involves recognizing food, gripping with the tail and turning towards the prey. Food is then conveyed to the mouth and swallowed.
2. Worms are still able to ingest food in the absence of the brain using local reflexes.
3. Central control is abolished in areas posterior to cuts through the body wall.
4. Functional recovery of behavior occurs in a minimum of 8 hr following closure of the wound.
5. Anatomical fusion of cut nerves occurs and conduction of potentials can be demonstrated across the healed cut regions of major nerves.
6. Recovery of function also occurs in approximately 36 to 48 hr if the cut is not allowed to heal suggesting that new or normally unused pathways can be recruited.

LITERATURE CITED

- ASH, J. F., W. O. McCLURE, AND J. HIRSCH, 1973. Chemical studies of a factor which elicits feeding behavior in *Dugesia dorotocephala*. *Anim. Behav.*, **21**: 796-800.
- BAYLOR, J. G., AND J. G. NICHOLLS, 1971. Patterns of regeneration between individual nerve cells in the central nervous system of the leech. *Nature*, **232**: 268-279.
- CHEN, P., AND H. KOOPOWITZ, 1972. The ultrastructure of neuromuscular systems in *Notoplana acticola*, a free-living flatworm. *Z. Zellforsch. Mikrosk. Anat.*, **133**: 277-288.
- DAVIS, W. J., G. J. MPITSOS, AND J. M. PINNEO, 1974a. The behavioral hierarchy of the mollusk *Pleurobranchaca*. I. The dominant position of feeding behavior. *J. Comp. Physiol.*, **90**: 225-243.
- DAVIS, W. J., G. J. MPITSOS, AND J. M. PINNEO, 1974b. The behavioral hierarchy of the mollusk *Pleurobranchaca*. II. Hormonal suppression of feeding associated with egg-laying. *J. Comp. Physiol.*, **90**: 225-243.
- FERNANDEZ, J. H., AND M. S. FERNANDEZ, 1974. Morphological evidence of an experimentally induced synaptic field. *Nature*, **251**: 428.
- GRUBER, S. A., AND D. EWER, 1962. Observations on the myo-neural physiology of the polyclad, *Planocera gilchristi*. *J. Exp. Biol.*, **39**: 459-477.
- HOY, R. R., 1973. The curious nature of degeneration and regeneration in motor neurons and central connectives of the crayfish. Pages 203-232 in D. Young, Ed., *Developmental neurobiology of arthropods*. Cambridge Univ. Press, London.
- JACOBSON, M., 1970. *Developmental neurobiology*. Holt, Rinehart and Winston, New York. 465 pp.
- JANSEN, J. K. S., AND J. G. NICHOLLS, 1972. Regeneration and changes in synaptic connections between individual nerve cells in the central nervous system of the leech. *Proc. Nat. Acad. Sci. U.S.A.*, **69**: 636-639.
- JANSEN, J. K. S., K. J. MULLER, AND J. G. NICHOLLS, 1974. Persistent modification of synaptic interactions between sensory and motor nerve cells following lesions in central nervous system of leech. *J. Physiol.*, **242**: 289-305.
- KOOPOWITZ, H., 1970. Feeding behavior and the role of the brain in the polyclad flatworm *Planocera gilchristi*. *Anim. Behav.*, **18**: 31-35.
- KOOPOWITZ, H., 1973. Primitive nervous systems. A sensory nerve net in the polyclad flatworm *Notoplana acticola*. *Biol. Bull.*, **145**: 352-359.

- KOPOWITZ, H., 1975a. Activity and habituation in the brain of the polyclad flatworm *Freemania litoricola*. *J. Exp. Biol.*, **62**: 455-467.
- KOPOWITZ, H., 1975b. Electrophysiology of the peripheral nerve net in the polyclad flatworm *Freemania litoricola*. *J. Exp. Biol.*, **62**: 469-479.
- KOPOWITZ, H., D. SILVER, AND G. ROSE, 1975. Neuronal plasticity and recovery of function in a polyclad flatworm. *Nature*, **256**: 737-738.
- LOEB, J., 1894. Beiträge zur Gehirnhysiologie der Würmer. *Pflügers Arch. Gesamte. Physiol. Menschen Tiere*, **56**: 247-269.
- NORLANDER, R. H., AND M. SINGER, 1972. Electron microscopy of severed motor fibers in the crayfish. *Z. Zellforsch. Mikrosk. Anat.*, **126**: 157-181.
- OLMSTEAD, J. M. D., 1922. The role of the nervous system in the regeneration of polyclad turbellaria. *J. Exp. Zool.*, **36**: 49-56.
- SAMUEL, E. P., 1953. Towards controllable silver staining. *J. Anat.*, **87**: 511-517.